OBSERVATIONS ON THE NATURAL HISTORY OF *POLYODON SPATHULA*

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DURING the springs of 1904 and 1905 I visited the regions in which Polyodon attains its largest size and occurs in greatest abundance. I had been aware for several years of the existence of this fish in great numbers in the lakes bordering the lower Mississippi River. On mentioning this fact to Professor Bashford Dean, he suggested to me the desirability of visiting these lakes with the object of obtaining the eggs and developmental stages of this peculiar fish. My best thanks are due Professor Dean for this suggestion, and for placing at my disposal during both years the Dyckman Fund of the Zoological Department of Columbia University with which to defray the expenses of the trips.

Most vertebrate embryologists and particularly those familiar with the development of the ganoids will admit, I believe, that a knowledge of the development of Polyodon is greatly desired. The ganoids at present furnish an almost complete and one of the most instructive comparative embryological series. The series is incomplete, however, in that nothing is known of the development of either member of the order Selachostomi. This order comprises only two species, *Polyodon spathula* and *Psephurus gladius*. The former is found in the Mississippi River and its tributaries; the latter is known only in some of the rivers of China. Thus they have a decidedly discontinuous geographical distribution.

I spent from March first to April fifteenth, 1904, in Concordia and Catahoula Parishes of Louisiana, and from April first until May eighteenth, 1905, in Washington County, Mississippi, and on the White River in Arkansas. During this entire time efforts were made to obtain spawning Polyodon. Although unfortunately I failed to secure any of the embryonic stages, I succeeded, during the three months on the lakes and rivers where this fish is so abundant, in making many observations on its habits. The present paper contains a brief account of the behavior of the fish

during the spring and early summer seasons, and conveys some idea of the great fishing industry to which it has given rise within the past twelve years.

DESCRIPTION OF POLYODON

Polyodon in the lakes bordering the lower Mississippi River attains a much greater size than in the Ohio and upper Mississippi River region. Museum specimens and those obtained in the more northern parts of their range are rather small fishes. In the metropolis of their distribution, however, they often attain a length of almost six feet, the longest one observed by the writer being five feet and nine inches from the tip of the tail to the end of the snout. Their weight often exceeds one hundred pounds; one hundred and forty-two pounds was the maximum record in Lake Washington, Mississippi, where the fish were larger than in any other lake visited.

The shape of Polyodon is shown in the accompanying photograph, Fig. 1. Note the contrast between the slender shark-like form of the middle individual, which is a characteristic river-fish, and the heavily proportioned body of the lake-fish, on either side.

The color of these fishes during the spring differs only slightly from that at other seasons. The back and dorso-lateral portions are of a steel or slate-like hue while the ventral and ventro-lateral parts are a glistening milk-white. The fins of most mature individuals show a delicate tinge of salmon-pink, but in others the fin color partakes of the general slate-like appearance of the dorsal portions. The general color of several fishes that were obtained shortly after spawning was of a peculiar reddish tint, being several shades lighter than the normal slate color. In two "spent" individuals this color difference was detected as they swam in the water before being lifted from the seine. The anal region of these fishes showed a dark purplish-red color and their ovaries gave unmistakable evidence that spawning had occurred. No indication of sexual dimorphism could be detected, the males and females being indistinguishable in their color, size, and shape, and in the proportions of their external body appendages. A female with

her ovaries filled with eggs of the season was usually recognized by the distended condition of the abdomen and yet even this distinction was not always valid since the males when fat and in good con-

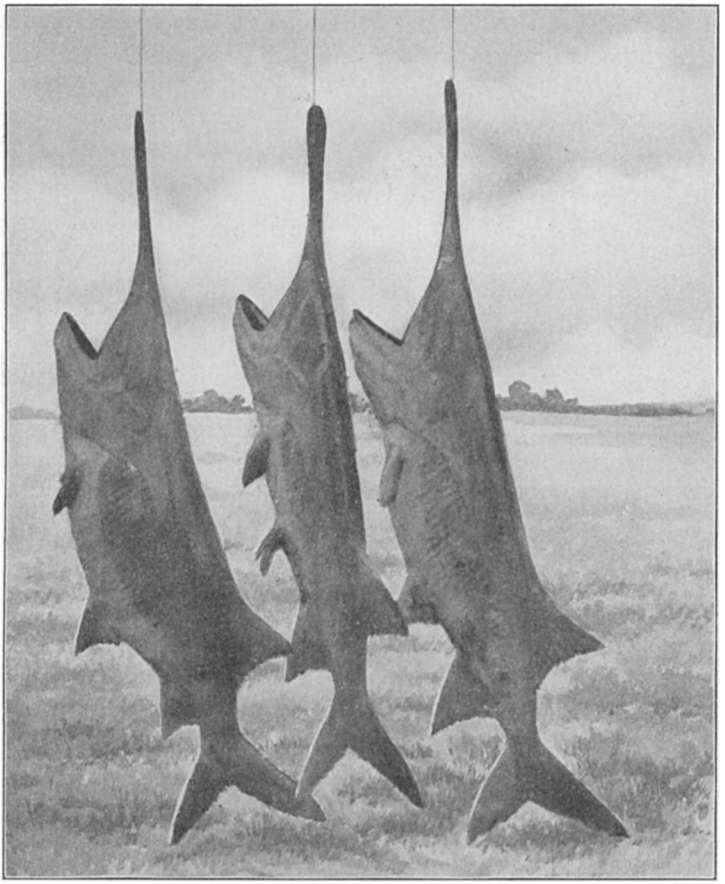

FIG. 1. — Three large specimens of Polyodon. The middle fish, from the river, is thin and slender, showing a torn fin and scars received while migrating. In contrast, the lake-fishes on either side are fat and well rounded, the one on the left showing an unusually distended abdomen although it is a male.

dition have so extensive a mass of adipose tissue about the testes that their abdomen is almost equally swollen. The fat about the testes of one male was found to weigh three and three-quarters pounds.

The larger females contain an enormous number of eggs. Sixteen pounds of roe was the heaviest single yield observed, but the maximum is no doubt greater; ten to twelve pounds was an average yield. The egg resembles that of Acipenser very closely in size and color. It is slightly oval in shape with the polar diameter longer and measuring about 2.7 mm.; the equatorial diameter is only about 2.2 mm. It is of a dark brown or blackish color. There is a considerable polar differentiation, the animal pole of the egg having a cap of lighter colored protoplasmic material with a rather distinct dark ring about its lower border. The denser deutoplasmic part of the egg is gradually located about its lower, vegetal pole.

Various measurements were made on a number of fish in the hope of discovering some sexual difference. While making such measurements a rather interesting ratio was found to exist between the length of the fish and that of the snout, as will be seen by referring to the accompanying table. In the table the individuals are arranged in the order of their lengths, the longest fish being at the top of the column. The entire length of the fish is expressed in inches in the first column and the length of the rostrum, from the anterior border of the eye to the tip of the snout, in the third column; by dividing the latter measurement by the former in any one case, the decimal given in the fifth column is obtained. The decimal, then, represents the fraction of the entire body length which is formed by the snout, and it is seen by comparing the data given for fifteen individuals selected at random, that the proportionate length of the snout decreases gradually and quite regularly as the fish increases in size. In other words a small fish, about two feet in length, has a snout one-third of the length of its body or eight inches long; and the large fishes, like the third and eighth individuals of the table, may have snouts less than one-fourth of their body lengths. Between these extremes one finds a regular gradation as is shown in the fifth column of the table.

TABLE I.

Length in inches	Sex	Length of rostrum	Weight	Proportion of rostrum length to body length	Remarks
69	♀	17.87	——	.258	Lake fish. 8 lbs. eggs.
67	♂	17.00	43 lbs.	.253	Lake-fish.
66	♀	15.75	41 "	.238	River-fish.
63	♂	16.50	62 "	.264	Lake-fish.
63	♀	15.75	90 "	.250	Lake-fish. 12 lbs. eggs.
62	♀	16.00	57 "	.258	Lake-fish.
60	♂	15.90	54 "	.266	Lake-fish.
59	♂	14.00	50 "	.237	Lake-fish.
53	♀	13.50	23 "	.254	River-fish.
51	♂	13.50	——	.265	Lake-fish.
49	♀	13.10	31 "	.267	Lake-fish.
44	♀	12.00	25 "	.272	Lake-fish.
36	♀	10.20	18 "	.283	Lake-fish.
30	♂	9.00	——	.300	Lake-fish.
24	♂	8.00	——	.333	Lake-fish.

By means of the above proportion one may calculate approximately the size of a fish from a small drawing. To test this I measured and calculated the proportion of length of rostrum to length of body in the Polyodon figured in Jordan and Evermann's Pl. XX, figs. 43 and 43a; the proportion found was .327 which according to the table would indicate that the specimen was about twenty-five or twenty-six inches long. Calculating from the inch line which accompanied the figure I found that the specimen was 27.2 inches in length, a very close agreement with my expectation.

From a few comparisons made between fishes living in the lakes and those in the river, it appears that the river fish have shorter and broader snouts in proportion to their entire body length than those living in Lake Washington.

HAUNTS AND HABITS OF POLYDON

The lakes in which these fishes are found in great abundance are the old "cut off" lakes of the Mississippi River. These crescent or horse-shoe shaped bodies of water were formed from time to time as the course of the river changed. Some of them are at present almost completely separated from the river, being connected only by a long chain of bayous and lagoons, oftentimes

almost one hundred miles in length. Other such lakes still retain a direct connection with the river and are termed by the fishermen "river-lakes." In these there is a current which often becomes very strong during the spring freshets, when the water of the Mississippi River rises.

Lake Louis in Catahoula Parish, Louisiana, is a very old lake, being now only from one to three hundred yards in width and about six miles long. During the spring floods the Ouachita River sends a large volume of "backwater" into it, sometimes causing it to rise as much as twenty feet. In many places the lake is from forty to fifty feet deep. Polyodon exists in this lake in large numbers, but it is an undesirable place for seining and therefore offers poor facilities for the study of the fish. Lake Washington in Washington County, Mississippi, is by far the richest source of Polyodon that I have been able to locate. This lake is a beautiful body of water more than one mile across in several places, and about twelve miles long. It connects with the Mississippi through about seventy miles of smaller lakes and bayous. As many as one hundred and fifty barrels of Polyodon have been caught in this lake at one haul of the enormous seine described below.

Polyodon, like most large fish, frequents the deeper portions of these lakes and is rarely caught in the shallower parts. It is almost never found in lakes less than ten feet in depth. Usually it is caught in those parts of the lakes having soft muddy bottoms, the sections with hard sandy bottoms yielding no Polyodon when seined. This is due to the feeding habits of the fish. The main diet of Polyodon consists of small Crustacea, usually copepods. These are very probably obtained by stirring the muddy bottoms and gulping in the agitated material, which is then effectively strained by means of the long slender gill-rakers, so that only the small arthropods remain in the mouth to be swallowed. One may often scrape more than a double-hand-full of these Entomostraca from the mouth of a Polyodon freshly brought up by the seine. The copepods were often alive, with their egg strings still intact, and in good condition for preservation. Jordan and Evermann state that "They (Polyodon) feed chiefly on mud and minute organisms contained in it, stirring it up with the spatulate snout." One must surmise from the general structure of the mouth and

gill-rakers that they feed on minute organisms, but Jordan and Evermann are surely in error, so far as my observations on some four hundred stomachs go, in stating that they feed chiefly upon mud. No doubt some fine mud or silt is taken into the throat along with the food, but it appears to be well strained out, since scarcely any mud has been found in the many stomachs examined.

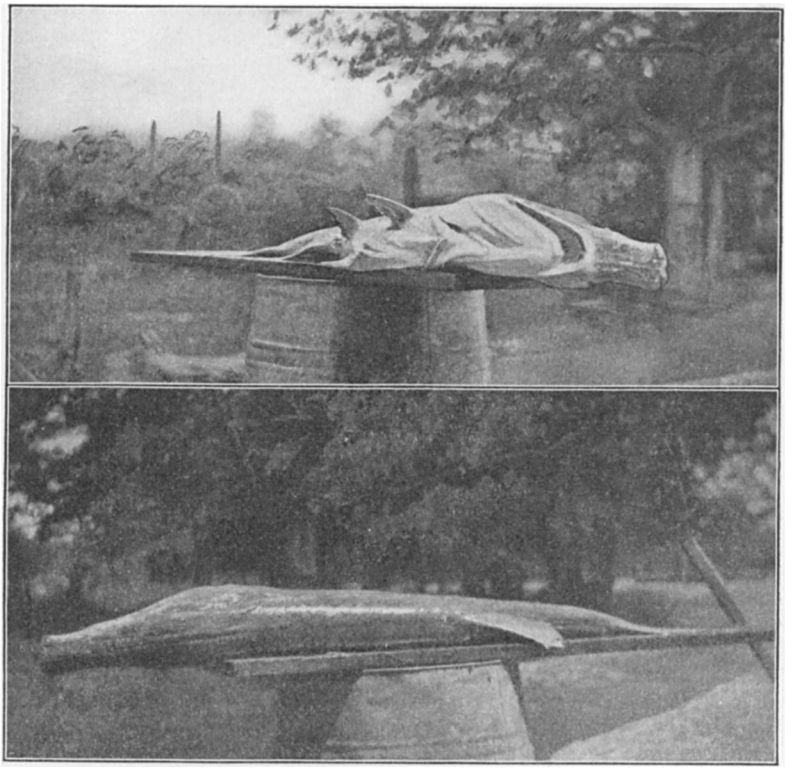

FIG. 2. — Ventral and dorsal views of a Polyodon measuring 4 feet and 7 inches. Its rostrum had been broken off during life and the wound had healed as seen in the photographs.

The contents of several stomachs were preserved in mass, and little if any silt has settled out from the animal material.

The function of the peculiar long rostrum or snout has not been definitely determined. There are some reasons for believing that the organ is used in procuring food but the following facts indicate that it is not essential for such a purpose. During the two springs

three specimens were found which had, through some mishap, been left with only stumps of their snouts. Fig. 2 shows a photograph of such a fish. In each case the fish was large, two being nearly four feet in length and the other measuring four feet and seven inches. In each the injured part of the snout was well healed, but no indication of regeneration of the organ was shown. It is evident from these individuals that this fish without the aid of its snout is capable of procuring food enough to maintain a large body. Moreover if the appendage was lost while they were yet small, they had succeeded in increasing in size without their "spatula with which to agitate the mud."

Fishermen state that large holes are often rooted out in the lake bottoms by the digging of Polyodon with its "paddle." In the bottoms of drained lakes, places resembling "hog-wallows" are found, which Polyodon is thought to have dug while feeding. Such statements are difficult to substantiate and yet there is probability that they are true, for there are immense numbers of Polyodon herded in one of these almost land-locked lakes, and they feed over the muddy bottoms.

Observations on the general behavior of this fish lead me to a rather skeptical position regarding the foraging value of the rostrum. I am inclined to regard it more as a tactile organ since the sense of sight is of so little use to the fish while swimming forward. Again its use for digging seems to be restricted as indicated by the actions of this fish when its rostrum strikes against any foreign object. When, for example, Polyodon is surrounded by a seine and happens to swim against the net at any place, it very often stops when its rostrum strikes the net; sometimes it continues to push forward by one or two indifferent efforts, and then gives up entirely, turning over on its back and floating along the cork-line of the seine. In a large haul fifteen or twenty fishes may be counted floating along the cork-line with their white ventral surfaces turned upward. Sometimes they may float thus on the outside of the seine and stupidly allow themselves to be picked up by the fisherman who guards the line in a row-boat, in order to catch the fish that float over while the seine is being hauled in. The larger and more active fishes often strike the seine several times before surrendering, but even they show but little ability

to back-off when their snouts strike against the net. From such actions one is led to think that if these fish should swim with much force into mud of a very viscid consistency, they would oftentimes be trapped, for from the above observations they appear too stupid to pull back and loose themselves. Since the fish lacks the power to turn its head from side to side, it cannot stir the mud with its spatulate snout, as Jordan and Evermann claim, but must agitate the silt by a general movement of its entire body. In this process the spatula no doubt plays an important rôle since it is a considerable portion of the anterior end of the body.

The food of Polyodon is extremely abundant in the lakes, and they grow to be very large and heavily proportioned in such places. One may distinguish almost at a glance between a fish that has lived in the lakes and one from the river; the latter is poor and slender as compared with the former. The lake-fish contains a much heavier roe, averaging ten or twelve pounds, whereas river-fish often have only three or four pounds.

The stomach of Polyodon, in addition to its crustacean diet, contains great numbers of a cestode parasite, *Dibothrium hastatum* (Linton). Hundreds of these little yellow-headed tape-worms measuring three or four inches in length are often present in a single stomach.

Polyodon like Lepidosteus is frequently seen to leap from the water during the spring; the leaping at this season is not so common, however, as it is later in the year. During the summer months one may often see several of these large fishes in the air at the same time. They make a vigorous jump, usually clearing the water entirely, and at times turning over backwards in the air so as to enter the water either head foremost or by striking on their backs. Apparently one fish may sometimes be seen to jump repeatedly at short intervals near the same spot. The object of such leaping is difficult to detect unless it be on account of the stagnant and poorly aerated condition of the water during the dry summer, when it becomes unusually low in these lakes.

Polyodon shows a considerable migratory tendency. During the spring, when the water of the Mississippi River rises for several feet and backs into the bayous, thus establishing connections with the large lakes, Polyodon begins immediately to come into the

lakes from the river and continues to come in large numbers so long as a sufficient connection is maintained. To do this it must often make long journeys through rather shallow water in which many obstructions, such as bushes and trees, are frequently met. Thus it finally reaches the lakes in a rather emaciated condition and with its body scarred and scratched. By referring again to Fig. 1 the river-fish in the middle will be seen to show such marks even in the photograph. It is equally true that the fish in the river-lakes (those lakes more directly connected with the river) migrate out into the river when the water begins to back in during the spring, so that fishermen often abandon their fishing in these places at such a season, since most of the desirable Polyodon have made their escape.

SPAWNING HABITS

I was unable, on either of my trips, to find fishes in a "running" condition or to locate a party in the act of spawning. By constantly watching the fish and taking numbers in the seine each day I concluded that the breeding season in this region occurs about the middle and latter half of April. The fish seem to breed only in running water, most probably in the bayous and small wooded lakes connected with the Mississippi River. My reasons for such conclusions may be gathered from the following observations.

During the first half of the month of April five females were taken which had their ovaries well filled with almost mature eggs. On April 4, 1905, three females of not unusually large size were examined and contained respectively sixteen, thirteen, and twelve pounds of roe. Such fish were taken in the lakes until shortly after the first of May when the following condition was observed. On May 5th a female five feet and nine inches in length, which weighed eighty pounds, was found to contain only eight pounds of eggs. Many of these eggs had taken on a whitish appearance and were very soft, so that on attempting to strip them from the ovarian membranes they broke and formed a milky pulp. After this time, fish from five different lakes were examined and all were found to be in a similar condition. Not one male Polyodon in any of the

lakes was found to be "running" although I examined from ten to twenty on almost every day from April 1st until May 13th, 1905.

A number of males and females were from time to time placed in a large wire-netting pen, with the object of keeping them until they reached the spawning condition. Some of these lived in the pen for four or five days but rarely longer, although the pen was twenty feet square and rested on the bottom of the lake. The larger ones are especially difficult to keep in confinement. The eggs of the confined females soon began to degenerate and soften, like those of the lake-females mentioned above.

After April 10th, 1905, the Mississippi River began to rise and river-fish were taken in Lake Washington after April 14th; several of these females on dissection were found to have spawned. The ovaries contained only a few defective eggs still attached to the membranes of their ventral border. The anal region was inflamed and other external appearances, such as their lighter pinkish color, made it practically certain that these fishes had deposited their eggs in a normal manner. I then concluded that the large fat lake-fish was unable to spawn in the still waters, and that its eggs were absorbed within its body after they began to degenerate. The males also seem to fail to arrive at the "running" stage, as none were observed in such a condition during either season.

An attempt was made to locate a spawning party in the running bayous leading into the river. On May 16th, 1905, great numbers of Polyodon were seen swimming and darting in all directions near the surface of the water in a small bayou in Washington County, Mississippi. This was the first time these fish had been observed swimming near the surface, and their spirited actions made one think them a spawning party. A zig-zag gill net one mile in length was dropped in the midst of these fish and within less than one hour one hundred and thirty-three large Polyodon had been lifted into the flat boat. On examination they proved to be river fish that were migrating up the bayou into the lake. All of the mature ones had apparently spawned some time before. They doubtless spawned near the mouth of this bayou which was about sixty miles distant, and with the rising water they began to swim up toward the lake. The fact that the lakes are so readily depleted of their stock of Polyodon by seining and are not again

able to repopulate themselves also indicates that the fish are non-productive in such places. Lakes that have been exhausted of Polyodon will remain so for years, unless the river rises sufficiently to permit the immigration of more fish to restock them.

Only one man was found who had probably observed Polyodon in the act of spawning. He related the way in which he had rowed a boat into a party of "Spoon-bills" during April several years before, and had succeeded in killing nine of them with an oar without being able to frighten them from the place. He said that this occurred in the edge of a wooded overflow border of a bayou, several miles from where it ran into the river.

It is curious that Polyodon does not spawn in the large clear-water lakes since the related *Lepidosteus osseus* and *L. tristoechus*, both being ganoids abundant in this region, spawn in great numbers in these lakes. A spawning place of Lepidosteus was visited on April 1st, 1905, though at this time only a few unhatched eggs remained and all of the larvae had swam away. The fisherman informed me that this party had spawned about March 15th. "Runners" of both species of Lepidosteus were taken in the seine until April 20th, so that their spawning season seems to continue here for several weeks.

METHODS OF CATCHING POLYODON

The commercial value of Polyodon is scarcely indicated in Jordan and Evermann's statement,— "the flesh [is] coarse, resembling that of the larger cat-fishes, but inferior in quality." For the past ten or twelve years the roe of Polyodon has been used as a commercial substitute for sturgeon caviar. Generally the Polyodon eggs are mixed with those of the sturgeon, so that the less attractive flavor of the former is not so evident. The flesh of Polyodon is shipped to the northern cities where it is dried or smoked and sold in the markets as dried sturgeon. The rapid decrease in the supply of sturgeon for the last ten or fifteen years has caused a strong demand on the part of the dealers for a substitute, and until now Polyodon is the only one successfully tried. The demand for Polyodon has caused an extensive fishing industry

to spring up in the lower Mississippi River region, until it has become the most valuable fish of these waters. This fishing industry is conducted in various degrees of perfection, and some of the more intelligent fishermen have very extensive apparatus for procuring Polyodon. On Lake Washington, Mr. McGehee, through whose kindness I was enabled to make most of the obser-

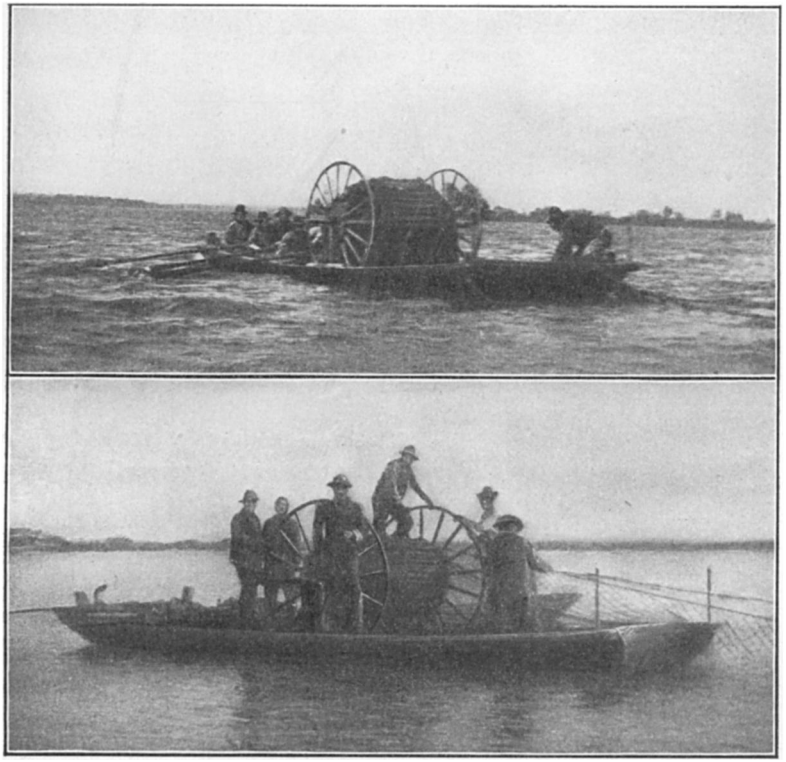

FIG. 3. — The upper photograph shows a crew of Polyodon fishermen putting out a seine almost two miles in length; in the lower photograph they are winding it in on the reel.

vations above recorded, directs a most efficient fishery. He runs two seines, one nearly two miles long and thirty feet deep, the other about one mile long and fifteen feet deep, for use in shallower water. These huge seines are wound upon a large reel which is constructed on a heavy barge. In laying out the seine for the catch, the barge is towed by a gas launch around a circular area

more than a mile in circumference. The barge is then securely anchored and a crew of about a dozen men proceed to wind in the seine by means of the reel, as shown in the photograph, Fig. 3. It requires usually about four hours to haul the seine. Great numbers of Polyodon are caught in such a manner, more than one hundred and fifty barrels bring the record for a single haul in Lake Washington.

The roe or caviar is much more valuable than the flesh of the fish, and during my stay on these lakes there was an average of one caviar fish to every twenty-four other individuals. The roe is taken from the fish enclosed in the ovarian membranes and then strained through a screen which serves to separate the eggs. A liberal amount of a calcium-free sodium-chlorid salt is then added, and the eggs are packed in kegs for shipment to the markets. One fisherman may ship as many as seventy-five of these hundred and fifty pound kegs in a single season, from November to April. At such a rate one is not surprised to learn that Polyodon has decreased greatly in numbers since the beginning of this new industry. At present many lakes that were formerly crowded with these fish are completely depopulated. The methods of seining are very exhaustive and as above mentioned the lakes are only restocked when the river rises sufficiently, which may not occur for a period of several years. River seining is almost impossible owing to the strong currents. This industry though in its infancy is decidedly on the wane; many of the most prosperous fishermen have now abandoned it entirely on account of the great decrease in the number of fish. Such an extensive apparatus is essential for taking the large Polyodon that the fishing is unprofitable unless they are caught in great numbers.

As I have stated, my attempt to secure material for a study of the embryonic history of Polyodon was unsuccessful. The observations presented in this paper, however, indicate when and how such material may be obtained. I expect to visit these regions again and to arrange with some well equipped fisherman to seine one of the running water lakes so that fish may easily be taken during the entire season. Thus it is hoped that the desired material may be procured.

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